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Factors influencing the distribution of *Cactoblastis cactorum*, a biological control agent of *Opuntia stricta* in Kruger National Park, South Africa

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Abstract

Cactoblastis cactorum, a phycitid moth, has been used with considerable success as a biological control agent against several different cactus species in many parts of the world, including *Opuntia stricta* in Kruger National Park [KNP], South Africa. Although the moth has become widespread and abundant in KNP, its populations have not reached levels where it is able to provide the desired level of control on the alien species which has invaded more than 35 000 ha of the park and continues to spread. Although several factors, especially acquired predators and parasitoids, are known to curb the abundance of *C. cactorum* in South Africa, the extent to which this applies in KNP is unknown. Logistic regression and Canonical Community Analysis were used to determine the biotic and abiotic factors affecting the distribution and abundance of *C. cactorum* in KNP. To do this, maps of the ranges of the insect and host plant were constructed and integrated with other environmental features. The logistic regression showed that *O. stricta* density had no influence on whether or not *C. cactorum* was present in an area. The Canonical Community Analysis suggested that a high fire frequency, the herbicide control programme and the presence of small host plants may be important in limiting the distribution of *C. cactorum*, either directly or indirectly, through impacts on associated predators or parasitoids.
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1. Introduction

Over the past 50 years *Opuntia stricta* (Haworth) Haworth has spread into an area of approximately 35 000 ha within Kruger National Park [KNP] in South Africa (Foxcroft et al., 2004), forming impenetrable thickets which smother indigenous vegetation and restrict movement of animals (Lotter and Hoffmann, 1998). Centred on Skukuza, from where the invasion was reported to have started (Zeller, 1996; Lotter and Hoffmann, 1998), the adventive population radiates out approximately 20 km in all directions. Of the area invaded, 2000 ha are regarded as densely covered, 17 000 ha as moderately dense and the rest as relatively sparse (Lotter, 1997). Initial attempts to control the spread of the plants depended largely on herbicidal applications but more recently the emphasis has shifted to reliance on biological control (Lotter and Hoffmann, 1998).

The disassociation of translocated plants from their specialist natural enemies, which continually damage native species in their natural habitats, is frequently invoked to explain why alien plants become invasive (Keane and Crawley, 2002). This seems to have been the case for various introduced cacti that have become problematic in many countries around the world. *O. stricta*, which originates in the south-eastern parts of North America is among the most troublesome of these translocated cactus species (Dodd, 1940).

At least 10 insect species utilise *O. stricta* as a food source in its native distribution range, some exclusively (Mann, 1969). Besides these natural associations, *O. stricta* is used as a host by two moth species, *Cactoblastis cactorum* (Berg) and *Cactoblastis doddi* (Heinrich), both of which are of South

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American origin but have been used for biological control of the plant in foreign lands (Dodd, 1940). *O. stricta* has recently become one of the most common hosts of *C. cactorum* in Florida, USA, where the moth is a recent inadvertent introduction (Johnson and Stiling, 1998; Soberon et al., 2001; Hight et al., 2002).

The affinity that *C. cactorum* has for *O. stricta* accounts for the success of the moth as a biocontrol agent in Australia (Dodd, 1940). By contrast, *C. cactorum* has had only a limited impact on *O. stricta* in South Africa (Hoffmann et al., 1998a,b). Several studies have been initiated to provide explanations for this relative failure and a diversity of possible causes have been identified. Baboons (*Papio ursinus*) and, to a lesser degree, vervet monkeys (*Chlorocebus aethiops*) were reported by Pettey (1948) to tear open infested cladodes and eat the adult larvae inside the cladodes. This habit was also observed in the KNP, specifically during the droughts in the early 1990s (Moran et al., 1994) and this type of damage continues to be evident. Rodents, spiders, fungi and other insect predators reportedly also affect *C. cactorum* populations by preying on the different life stages (Pettey, 1948). Some of these predators are localised and scarce, so their impact is minimal. By contrast, at least six species of ants have a substantial impact on *C. cactorum* populations by preying on the eggs of the moth over wide areas (Pettey, 1948; Hoffmann and Zimmermann, 1989; Robertson and Hoffmann, 1989).

Besides the above causes, other factors may influence the current distribution and density of *C. cactorum*. Among these are the abundance and size of the host plants in conjunction with various environmental parameters. This paper reports on a study that was undertaken in KNP to determine how, and to what extent, the distribution and density of *C. cactorum* has been determined by properties of the host plant and the surrounding environment. The objective of the study was to provide insights into the relationship between the agent and its host to determine how best to exploit *C. cactorum* in the control operations against *O. stricta* in KNP.

2. Materials and methods

2.1. Study area and data collection

The study was conducted throughout the area affected by *O. stricta* in the southern region of the KNP, *viz*. 35 000 ha around Skukuza camp. Surveys were undertaken predominantly during routine control operations and during other *O. stricta* monitoring exercises from November 2000 to April 2002. The surveys are continuing for use in a long-term monitoring programme. Positions of all plants that were encountered were recorded by means of a GPS receiver (Geographic Positioning System; Garmin 12 XL, horizontal accuracy 7–15 m). At the same time the size of the *O. stricta* plants was measured (for details see Foxcroft et al., 2006-this volume), presence or absence of *C.cactorum*, substrate, water regime, distance to nearest *O. stricta* plant, proximity to roads and rivers, fire return frequency, past management history, soil form (SCWG, 1991), soil depth, soil clay content and vegetation type including, dominant woody vegetation type, percentage open areas and grass cover (Kemp et al., 1997).

Additional environmental features were obtained from the GIS (Geographic Information System) section in Skukuza. The environmental features were selected on the basis of potentially having a direct (vegetation and physical structure) or indirect (parasites and predators, e.g. ants) effect on *C. cactorum*.

2.2. Statistical processing and data analysis

Canonical Community Analysis [CCA] (Ter Braak, 1998) was carried out to establish patterns and associations between *C. cactorum* distribution and environmental factors. Species and environmental data were used to extract patterns from the explained variation (direct gradient analysis). The forward selection summary (in CANOCO) was also used, as this feature is useful for ranking environmental variables in importance thereby reducing a large set of environmental variables. The variables were selected automatically, where the *K* best variables are selected sequentially on the basis of maximum extra fit. Thereafter, the statistical significance of each selected variable was judged by a Monte Carlo permutation test. Monte Carlo permutation tests are frequently used to select a subset of variables that explain the species data nearly as well as the full data set for the construction of the CCA biplot (ordination diagram).

Observations that occur in one of two possible states, namely 0 and 1 (binary variables), require specialized techniques for analysis. For analysis of impacts of *O. stricta* density on presence and absence of *C. cactorum*, logistic regression analysis (GENSTAT) was used (Alvey, 1980). The method is based on the logistic transformation or logit of a proportion. In this case, the binary variable was the absence (0) or presence (1) of *C. cactorum*. In modelling this data, both actual distance (distance to nearest neighbour, measured in meters) and distance class (all records divided into categories), as a measure of density, were included as explanatory variables.

If there is heterogeneity in the data, in other words, the residual deviance is noticeably larger than its expected value, the ‘dispersion’ option of the model is used to request another value. Therefore, when fitting the model, the dispersion parameter was adjusted to 0.33. To determine whether a variable is significant or not, it is first added to the model and then excluded (backwards elimination). The resulting degrees of freedom associated with the change in deviance are then compared to Chi squared critical value to determine significance. The more important a variable is, the greater the change in deviance when the variable is excluded.

The presence and absence of *C. cactorum* was evaluated to determine whether there was a correlation between host plant density and the abundance of *C. cactorum*. Observed distance (plant density) and density classes were calculated to determine the most significant factor.

Other features of the habitat were analysed against the presence or absence of *C. cactorum.* This was to identify potential factors that may influence colonisation of an area by

Table 1
Difference in the change in deviation associated with *O. stricta* density and *O. stricta* density classes

Responsible variable	Change in degrees of freedom	Change in deviance	Chi square
Density classes	1	38.9421 *	3.841
Density	2	8.5096 *	5.991

In modelling the impact of *O. stricta* density on *C. cactorum* presence and abundance, both the actual distance (distance to nearest neighbour, measured in meters) and distance class (all records divided into categories) as a measure of density, were included as explanatory variables. The more important the variable is, the greater the change in deviance when excluding this variable.
* Significant at the 95% level.

C. cactorum and hence its ability to control *O. stricta* over the entire range of the weed within KNP.

3. Results

3.1. O. stricta density and occurrence of C. cactorum

Density class categories and not the observed distances between plants (= relative density measurements) caused the greatest change in deviance when this variable was excluded from the model (Table 1). As a result, the density class categories were used to measure the impact of *O. stricta* density on the presence or absence of *C. cactorum*.

O. stricta density had no influence on the occurrence of *C. cactorum* (Fig. 1). The distribution of observations at points 1.0 and 0.0 (*C. cactorum* presence and absence respectively) is uniform, with no clumping tendency at any particular density class. Therefore, *C. cactorum* is equally likely to occur in an area regardless of *O. stricta* density. The fitted model (solid line) indicates no significant trend towards either presence or absence at any density class.

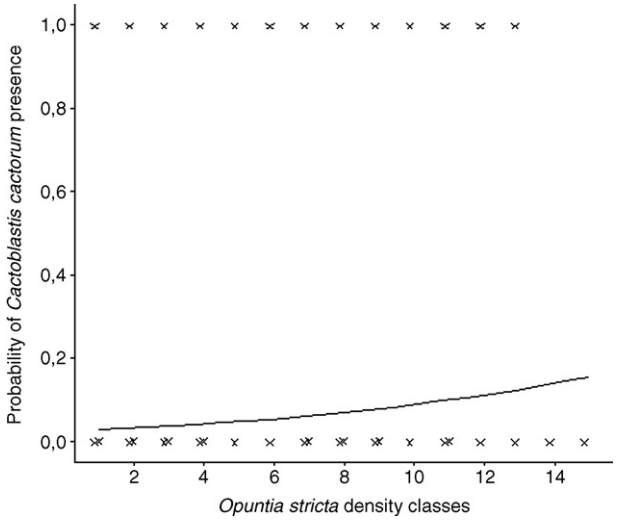

Fig. 1. The probability of *C. cactorum* presence at different *O. stricta* density classes. Point 1.0 and 0.0 represents *C. cactorum* presence and absence respectively, and represent the real observations (collected data represented by X). The smooth line indicates the fitted model.

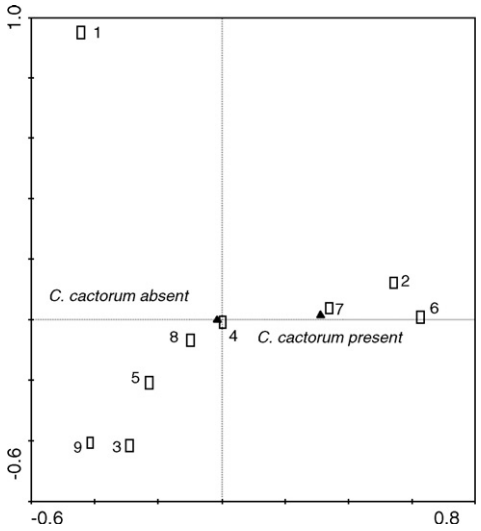

Fig. 2. Canonical Community Analysis (CCA) diagram (scaling: interspecies distance; standardisation by species-centred and standardisation by samples-centred), which indicates the impact of the environmental variables on the distribution and abundance of *C. cactorum*. (▲ *C. cactorum* presence/absence; □ plots).

3.2. Environmental factors and occurrence of C. cactorum

The association between the presence or absence of *C. cactorum* and plots is clearly divided on the horizontal axis (Fig. 2). Although a close association appears to exist between the presence of *C. cactorum* and plot 7, and to a lesser degree plot 2 and 6, these relationships are tenuous and provide no clear explanation for the observed patterns (eigen value of 0.03; Table 2). No factors are significantly present in any specific plot to enable generalisation about factors influencing presence of

Table 2
Monte Carlo significance test (199 permutations under reduced model)

Axes	1	2	3	4	Total inertia
Eigen values	0.030	0.000	0.000	0.000	0.030
Species–environment correlations	0.999	0.000	0.000	0.000	
Cumulative percentage variance					
of species data	98.8	100.0	0.00	0.00	
of species–environment relation	100.0	0.00	0.00	0.00	
Sum of all unconstrained eigen values:					0.030
Sum of all canonical eigen values:					0.030

Monte Carlo significance test

Test of significance of first canonical axis: Eigen value=0.030
F-ratio=0.000
p-value=1.0000
Test of significance of all canonical axes: Trace=0.030
F-ratio=0.000
p-value=1.0000

Eigen values are given between 0 and 1 and explain the % variance accounted for by that axis.

Table 3
Forward selection (FS) summary of data analysed that might potentially impact on *C. cactorum* presence and absence

Variable	Conditional effects			
	Var. N	Lambda	*p*	*F*
O. stricta plant size: 230–400 cladodes (size6)	13	0.01	0.038	6.65
Acacia woodlands/mixed bush (domwd2)	25	0.01	0.01	9.46
O. stricta plant size: 11–35 cladodes (size2)	10	0.01	0.04	7.69
Fire frequency; three fires out of 45 (fire3)	2	0	0.106	4.05
Fire frequency; five fires out of 45 (fire5)	4	0	0.272	1.74
Dry grassland (h1)	17	0	0.318	1

Var. N indicates the variable number; Lambda values provide a test of significance for the squared canonical correlation; *p*-values are based on 499 Monte Carlo permutations under the reduced model; the *F* statistic represents a test of the null hypothesis that the expected values of the regression coefficients are equal to each other and that they equal zero.

C. cactorum. This in the same way applies for *C. cactorum* absence.

Analysis of the forward selection summary (Table 3) showed that *C. cactorum* was significantly more often present where there were large plants (size 6, 230–400 cladodes) ($p=0.038$ and Lambda=0.01) and in *Acacia* woodlands/mixed bush (domwd2) ($p=0.01$ and Lambda=0.01).

4. Discussion

Johnson and Stiling (1998) report on the ability of *C. cactorum* to disperse over considerable distances in a short space of time (up to 240 km per year) in Florida. However, Dodd (1940) indicated that in Australia the moth only spread 16–24 km unaided from the release point in approximately 2.5 years. Pettey (1948) also reported a modest rate of dispersal in South Africa, where the moth moved only 3–6 km in 2.5 years within *Opuntia ficus-indica* infestations. A distance of 30–40 km from one extremity of the KNP *O. stricta* infestation to the other should have been traversed readily by *C. cactorum* over a period of 14 years. In spite of the continued presence of *C. cactorum* in KNP (Hoffmann et al., 1998a,b) the invaded area in the park is increasing rapidly, with uncharted dense clumps of *O. stricta* being discovered at regular intervals.

This study showed that *C. cactorum* is more likely to occur where there are larger plants. However, the herbicidal control programme explicitly focuses on the control of large, fruiting plants, to prevent long-range dispersal of seeds by the primary dispersal agents (baboons and elephants). This possibly attests to the fact that the integration of herbicides and biocontrol can be extremely difficult, with one control method impacting negatively on another.

Although *C. cactorum* was recorded more frequently in fine-leaved (*Acacia*)/mixed woodlands, this could be due to an overlap between the two mixed woodland categories and indicate only a partial preference for the fine-leaved woodland. Alternatively, there may be a relationship with some factor that is present or related to *Acacia* woodland, such as vegetation density, position on slope, grass biomass and associated fire frequency and intensity.

After 14 years *C. cactorum* has caused considerable damage on the target weed, but has never realised its full potential as a biological control agent of *O. stricta* in KNP (Hoffmann et al., 1998a,b). Although the moth has persisted and become widespread its population levels are too low for it to be sufficiently damaging to bring the weed under control on its own. There is little doubt that predators and parasitoids continue to suppress populations of the insects. However, other contributory factors have been identified in this study, including features of the host plants and the habitats in which they grow. These findings, in combination with previously reported work, show that the limitations of *C. cactorum* cannot be rectified in this instance and further control agents are needed if biological control of the weed is to be improved. A more-recently released cochineal insect (*Dactylopius opuntiae*) is filling this role and showing considerable promise so far.

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